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THE IDENTITY AND NOMENCLATURE OF THE PACIFIC NORTH AMERICAN SPECIES *ZELTNERA MUHLENBERGII* (GENTIANACEAE) AND ITS DISTINCTION FROM *CENTAURIUM TENUIFLORUM* AND OTHER SPECIES WITH WHICH IT HAS BEEN CONFUSED

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Abstract

The name *Zeltnera muhlenbergii* (Griseb.) G. Mansion is here applied to a species native from Monterey County, California, to southwestern British Columbia. From *Z. davyi* (Jeps.) G. Mansion, a California endemic to which the name *Z. muhlenbergii* has sometimes been misapplied, *Z. muhlenbergii* differs in that its calyx lobes are not keeled or have keels proximally only, to 0.25 mm wide, and its corolla lobes are 1–2 mm wide; in *Z. davyi* the keels of the calyx lobes are 0.3–0.6 mm wide and the corolla lobes are 2–3 mm wide. *Zeltnera muhlenbergii* has often been confused with *Centaurium tenuiflorum* (Hoffmanns. & Link) Fritsch ex Janch. *s.l.*, a species naturalized from Eurasia, now established in Pacific and Gulf coastal North America. From *C. tenuiflorum*, *Z. muhlenbergii* differs most notably in its flabelliform rather than ovate stigmatic lobes and in its more open, non-corymboid cymes.

Key Words: California, *Centaurium*, Gentianaceae, nomenclature, taxonomy, *Zeltnera*.

Centaurium Hill *s.l.* was recently divided by Mansion (2004; Mansion and Struwe 2004) into four genera, two of which are pertinent to the present discussion. The species native to North America north of Mexico were placed in *Zeltnera* G. Mansion and the naturalized species discussed here were retained in *Centaurium*. Although Mansion's division of *Centaurium* was based largely on nrDNA and cpDNA sequences, Broome (1973) had commented earlier that "the New and the Old World taxa (of *Centaurium s.l.*) have totally different constellations of characters." The name *Zeltnera* is used here for the accepted identifications of native species. Except for the gender endings, the specific epithets remain the same whether the respective species are placed in *Erythraea* Borkh., *Centaurium*, or *Zeltnera*. (The genus name *Erythraea*, with its authorship variously attributed, was widely used for *Centaurium s.l.* during the nineteenth century, prior to a consensus as to the effective and valid publication of the genus name *Centaurium* Hill [Heller 1908], but is no longer in use.)

Taxonomic treatments of *Centaurium s.l.* in North America differ greatly. Among them, discrepant applications of the name *C. muhlenbergii* (Griseb.) W. Wight ex Piper have led to uncertainty as to whether plants so designated constitute a native species appropriately of conservation concern or an introduced species of which the North American range is expanding. This paper discusses the correct application of the name *Zeltnera muhlenbergii* (Griseb.) G. Mansion, distinguishes *Z. muhlenbergii* from the species with which it has been confused, correlates historic applications of names with the nomenclature accepted here, and provides a published equivalent to the personal communication from me cited by Mansion (2004). Specimens examined include those of the *Zeltnera* and naturalized *Centaurium* species from North America north of Mexico, or those of the species discussed in this paper, at BM, CAN, CHSC, DAO, DUKE, GH, HAM, ILL, JEPS, K, MICH, MO, NY, OSH, TRT, and UC.

Typification of the Name *Zeltnera muhlenbergii*

In the original description of *Erythraea muhlenbergii*, Grisebach (1838) cited specimens collected by Gotthilf Henry Ernest Muhlenberg in Pennsylvania and by David Douglas in California. He also cited "*E. Centaurium* Beck" (i.e., (L.) Pers. *sensu* Beck [1833], who had thus identified plants from New York), but he expressed uncertainty as to whether Beck's New York plants were of the same species. In 1839, Hooker and Arnott (in Hooker and Arnott 1830–1841) identified Beck's plants as *E. ramosissima* Pers. (=*Centaurium pulchellum* (Sw.) Hayek ex Hand.-Mazz. et al., a species native to Eurasia, naturalized in North and South America and Australia; the epithet *ramosissima*, illegitimate under current rules of nomenclature, was subsequently displaced in general use for this species by the earlier, legitimate epithet *pulchella*). Gray (1848) placed the Pennsylvania component of Grisebach's *E. muhlenbergii* in the synonymy of *E. ramosissima*. These identifications have

consistently been accepted (as *C. pulchellum*) by later authors. Torrey (1857), who was aware of the exclusion of the eastern plants by previous authors, accepted the name *E. muhlenbergii* "quoad pl. Calif." for plants from Benicia, Solano Co., California. In the interim Wood (1845 and later editions) had given "N.Y., Penn." as states in which *E. muhlenbergii* occurred, without mentioning California, but because the early editions of Wood's *Class-Book of Botany* did not cover western North America and the later editions included only selected western species, he did not address the question of whether the eastern and western specimens cited by Grisebach as *E. muhlenbergii* were conspecific. Later authors have not interpreted Wood's treatment as having restricted the circumscription of *E. muhlenbergii* by excluding the California specimens.

Gray (1876, 1878) explicitly excluded both Beck's and Muhlenberg's specimens from *E. muhlenbergii*, despite the epithet, and retained the name for the only remaining element cited by Grisebach, Douglas's plants from California. Piper (1906) formalized this typification by citing Douglas's collection as the type, with no mention of Beck's or Muhlenberg's, and Gillett (1963), in accord with Grisebach's (1838) statement that he had seen the Douglas collection in the herbarium of W.J. Hooker, specified the component at K, into which repository Hooker's herbarium has been incorporated.

At K, plants perhaps from a single collection by Douglas (although C. Rose Broome expressed uncertainty in 1979 annotations) are present on two sheets. The specimen bearing the bar code number K000195655, is from W.J. Hooker's herbarium (Fig. 1), and is appropriately considered the lectotype. This is the only such collection from Hooker's herbarium, and it uniquely is labeled with a provisional name in handwriting identified by Otto Stapf (annotation) as Grisebach's and matching that in an attached note. This note, presumably sent by Grisebach to Hooker, states that he would henceforth use the name *E. muhlenbergii* ("*Mühlenbergii*") instead of the provisional name, and contains wording similar to that used by Grisebach (1838) in the original description of the species. The combination of the note and Grisebach's label bearing the provisional name indicates that Grisebach saw this specimen and called it *E. muhlenbergii* shortly before he published that name in 1838. On this herbarium sheet the name Douglas appears only in Grisebach's note and in a 1979 annotation by Broome, but Grisebach's citation of Douglas in both the note and his published description of the species indicates that he understood these plants to have been collected by Douglas, presumably from information provided by Hooker. A stigma recognizable as that of a *Zeltnera* species rather than a *Centaurium* (discussed below) is visible on one of these plants. The possibility that they represent Beck's or Muhlenberg's collection, or any naturalized species from New York or Pennsylvania, can thereby be eliminated from consideration.

The specimen on the other sheet at K, with the bar code number K000195658, is from George Bentham's herbarium, with the printed label "Douglas 1833." The date probably indicates when a shipment reached a recipient, as Douglas did not collect specimens in California in 1833 (McKelvey 1956). It also bears a label in Bentham's handwriting identifying it as *Erythraea*, with the original specific epithet crossed out and replaced with "*Muhlenbergii*," and the citation "Griseb. Gent. 146." In what may be a later annotation, Bentham added "[ditto] in DC. Prod. 9.60."

Typified by the Douglas collection at K, the name *Zeltnera muhlenbergii* is correctly applied to a species native to western North America from California north to southwestern British Columbia, with most of its populations in California. A representative well-developed plant of this species is illustrated in Figure 2. (Depending on conditions of the habitat and the time of seed germination in relation to photoperiod, plants of this and other *Zeltnera* species are sometimes smaller than well-developed plants, with shorter internodes and less dichasial branching, as in the type collection.) The distribution of *Z. muhlenbergii* in California is mapped in Figure 3. A few records exist from scattered localities farther north. Most Oregon records are from the western part of the state, but it is also known from Harney Co., Oregon, and from Washington Co. in adjacent Idaho. There are historic records from eastern Washington, but no recent collections from that state have been encountered in this study. The northernmost records are from Vancouver Island, British Columbia. All records of this species from Nevada appear to have been based on misidentified plants of *Z. exaltata*, *Z. namophila* (Reveal, C.R. Broome, & Beatley) G. Mansion, and perhaps other native species.

Identity of the Type Specimen: *Zeltnera muhlenbergii* vs. *Z. davyi*

Successive annotations by W. L. Jepson (in JEPS) reflect a change in his opinion as to the correct application of the name *Centaurium muhlenbergii*. His descriptions of *C. muhlenbergii* (Jepson 1901 [as *Erythraea*], 1911) and his original identification of *Jepson 7624* (JEPS), from Mendocino Co., California, as *C. muhlenbergii* indicate that initially he applied that name to the species called *Zeltnera muhlenbergii* in this paper. Later (annotations in 1935), he concluded that the name *C. muhlenbergii* was applicable,

FIG. 1. Holotype collection of the name *Erythraea muhlenbergii* Griseb. (*Douglas s.n.*, K).

instead, to the taxon he (Jepson 1925) had previously described as *C. exaltatum* var. *davyi* Jeps., a California endemic here treated as *Zeltnera davyi* (Jeps.) G. Mansion. He annotated the type of the latter name (cited below) as "true *C. muhlenbergii*!" with the statement that "*C. davyi* is exactly the original *C. muhlenbergii*! as compared at Kew, 1935." He reidentified *Ferguson & Ferguson 294* (JEPS; identified as *Z. davyi* in this study), which he had originally called *C. exaltatum* var. *davyi*, as *C. muhlenbergii*, with the comment "very close to Douglas type at Kew."

FIG. 2. Representative specimen of *Zeltnera muhlenbergii* (*Oswald & Ahart 9267A*, CHSC).

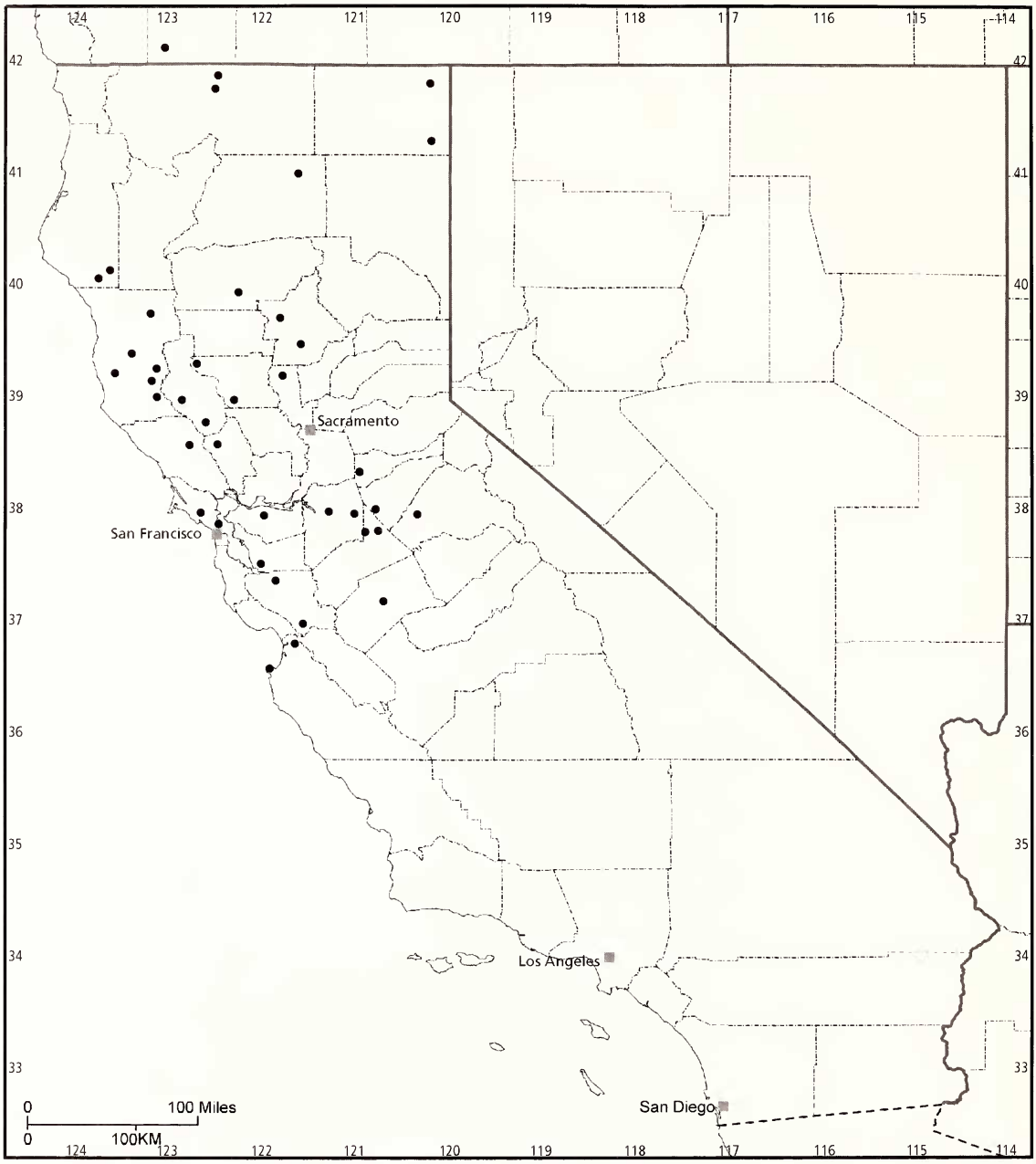

FIG. 3. Documented distribution of *Zeltnera muhlenbergii* in California.

Jepson 7624, he then stated (annotation), was not *C. muhlenbergii*, but was instead *C. floribundum* (Benth.) B. L. Rob., as he had determined from examining the type of the latter name at Kew. From 1935 on he applied the name *C. muhlenbergii* to the species called *Z. davyi* in this paper and the name *C. floribundum* to the taxon treated here as *Z. muhlenbergii*, and discontinued all use of the epithet *davyi*. (The name *C. floribundum*, interpreted here as a heterotypic synonym of *Z. muhlenbergii*, is discussed below.) More recently, C. Rose Broome and James L. Reveal (annotations in JEPS, MO, and UC in 1988, 1992, and undated, probably ca. 1980) likewise applied the name *C. floribundum* to the species treated here as *Z. muhlenbergii* and the name *C. muhlenbergii* to the species treated here as *Z. davyi*, whereas Hickman (1993), Beidleman and Kozloff (2003),

FIG. 4. Flowers of *Zeltnera* spp. a. Holotype, *Z. muhlenbergii*. b. *Z. muhlenbergii* (*Oswald & Ahart 9267A*, CHSC). c. *Z. davyi* (*West 140*, JEPS).

and Mansion (2004) retained the epithet *davyi* for the latter species.

Jepson (1925), as noted above, originally described the taxon *davyi* as a variety of *Centaurium exaltatum* (Griseb.) W. F. Wight ex Piper but later treated it as a distinct species, to which he applied the name *C. muhlenbergii*. Dunbar (1929) treated it as a variety of *C. curvistamineum* (Wittr.) Druce (species name discussed below; varietal combination unpublished), although his concept of var. *davyi* included some plants from eastern California referable to *Z. exaltata* (Griseb.) G. Mansion as well as plants identified as *Z. davyi* in this study. Abrams (1951) accorded the taxon the rank of species as *C. davyi* (Jeps.) Abrams. This status, including the distinctness of this species from the one treated here as *Z. muhlenbergii*, has generally been accepted by subsequent authors, including Munz and Keck (1959), Broome (1973), Hickman (1993), and Mansion (2004). Nevertheless, the species respectively designated *Z. davyi* (Figs. 4 and 5) and *Z. muhlenbergii* (Figs. 2 and 4) in this paper are often similar in aspect. The question as to which of these species is represented by the type of the name *Z. muhlenbergii* is addressed below.

The Douglas specimens at K ex herb. Bentham (as distinguished from those ex herb. Hooker) appear definitely to represent the species called *Z. muhlenbergii* in this paper rather than *Z. davyi*. This was acknowledged by Broome in an annotation in 1979. She likewise annotated the replicate at E in 1987. Determination that the Douglas specimens ex herb. Hooker also represent this species rather than *Z. davyi* has required careful examination. Plants that small are not ideal for identification, and the distal leaves are proportionately wide and broad-based, approaching in shape those more common in *Z. davyi*. In *Z. davyi* elliptic to ovate leaves generally retain their width (usually over 5 mm except on the smallest plants) well into the inflorescence, sometimes to the summit. In *Z. muhlenbergii* of this paper elliptic to narrowly ovate leaves, when present, are usually limited to the proximal third or less of the plant, with at least the distal leaves being narrower, but both species vary in leaf proportions and occasionally depart from these generalizations.

In the species here designated *Z. muhlenbergii*, the larger plants are usually branched from near but not at the base to the summit. Branches from the base are less common in *Z. muhlenbergii* than in *Z. davyi*, although not rare, and when present are often more slender than the main stem. The proximal branching of the inflorescence of *Z. muhlenbergii* is usually dichasial, with the central flower in the divisions sessile or on a pedicel to 5 mm or occasionally to 12 mm long on the larger plants. Distal branching is often monochasial, with a branch developing only on one side of each flower. The flowers in the distal portions of the inflorescences are sessile or on pedicels to 4 mm. The inflorescences of small plants are often monochasial throughout. In *Z. davyi*, medium-sized and larger plants are usually several-stemmed from the base, although smaller plants are often single-stemmed. The branching of the inflorescence is similar to that of *Z. muhlenbergii*, but pedicels (1.5) 4–25 mm are generally present even in the distal portions of the inflorescence. In the holotype collection of the name *Z. muhlenbergii*, one plant is basally several-stemmed and the other is single-stemmed, but with plants of that size the branches are too few and too short to exhibit the characteristic branching patterns of larger plants of the respective species, so this condition is of little

FIG. 5. Representative specimen of *Zeltnera davyi* (*West 140*, JEPS).

diagnostic value. On the type plants, pedicels sufficiently well exposed to be measured range from 4–5 mm in the proximal divisions of the inflorescence to ca. 1.5 mm distally, and, although not definitive, are compatible with the interpretation of *Z. muhlenbergii* in this paper.

Zeltnera davyi differs from all similar species in that the calyx lobes are distinctly keeled along the midveins for much of their length, with the keels of all or at least the outer lobes proximally being 0.3–0.6 mm wide, and the calyx consequently is ovoid to ellipsoid. In *Z. muhlenbergii*, in contrast, the keels are absent or weakly developed, if present being confined to the proximal plant of the calyx and less than 0.25 mm wide. The outer calyx lobes of the type plants of *Z. muhlenbergii* are slightly keeled near the base, but even there the keels are ca. 0.2 mm wide, and the calyx appears narrowly cylindric, as in *Z. muhlenbergii* of this paper. Calyces of one of the type plants and of representative plants of *Z. muhlenbergii* and *Z. davyi* are compared in Figure 4.

The corolla tube of *Z. davyi* flares at ca. 40° almost immediately above the summit of the ovary. That of *Z. muhlenbergii* at a comparable stage of floral development flares more gradually between the summit of the ovary and the base of the lobes, forming a longer, more distinct, slender neck (Fig. 4b, c). The corolla lobes of *Z. davyi* are ovate-oblong to ovate-elliptic, 3–7 × 2–3 mm, slightly less to more than half as long as the tube, rounded at the apex. Those of *Z. muhlenbergii* are lance-elliptic, 2–7 × 1–2 mm, less than half as long as the tube, tapering to a subacute apex. The corolla lobes of the type specimen that are pressed flat enough for measurement are 1–1.2 mm wide. In these floral characters, the flowers of the type plants are consistent with the interpretation of *Z. muhlenbergii* in this paper.

It has sometimes been assumed that Douglas collected the type of the name *E. muhlenbergii* in the vicinity of Monterey Bay, California, which is in the heart of the range of *Z. davyi* but at the southern limit of the range of the species called *Z. muhlenbergii* in this paper (Figs. 3 and 6). In that area, both species are known from Gilroy, and three replicates of *Elmer 4378* (JEPS, MICH, UC) suggest that intergradation or hybridization has occurred at Pacific Grove. Douglas did much of his California botanizing in the vicinity of Monterey Bay, but in 1831, at the time of year when *Z. muhlenbergii* would have been in flower, he traveled north from Monterey via the vicinity of San Francisco to the site of present-day Sonoma (McKelvey 1956), which is well within the range of the species interpreted here as *Z. muhlenbergii*.

I have, therefore, concluded that despite the relatively wide leaves of the type plants, the name *Z. muhlenbergii* is correctly applicable to the more northern of these two species, to which the name *Z. muhlenbergii* is therefore applied in the remainder of this paper. This conclusion preserves the widely accepted usage of the epithet *davyi*, including that by Abrams (1951), Munz and Keck (1959), Hickman (1993), Beidleman and Kozloff (2003), and Mansion (2004). It also preserves the well-established use of the epithet *muhlenbergii* for plants of British Columbia and Washington, e.g., by Piper (1906), Hitchcock (1959), Gillett (1963), Straley et al. (1985), Douglas (1999), and Kozloff (2005).

Heterotypic Synonymy of *Zeltnera muhlenbergii*

Nomenclatural complexity with regard to heterotypic synonyms of the name *Zeltnera muhelnbergii* has several causes. Initially, in some cases, variation within the species, or the failure to recognize plants of true *Z. muhlenbergii* as representing a species already described and named, has led to the publication of new, heterotypic names for the species as it is circumscribed here. Later, in such cases, the use of a heterotypic synonym for the true *Z. muhlenbergii* has been perpetuated, even though the circumscription of the species may have been equivalent to that accepted here, because the name *Centaurium muhlenbergii* had incorrectly become associated with some other species.

The name *Erythraea floribunda* Benth., treated by Holmgren (1984) as a heterotypic synonym of *C. muhlenbergii* and interpreted as such in this study, is typified by specimens collected "in valle Sacramento," California, by Karl Theodor Hartweg. As Holmgren recognized, these specimens represent the species treated here as *Z. muhlenbergii*. Although differences in plant size may have contributed to Bentham's (1849, in Bentham 1839–1857) perception that the specimens he identified, respectively, as *E. muhlenbergii* and *E. floribunda* represented different species, plants of the latter being larger, his concept of *E. muhlenbergii* appears to have been based in part on plants that would now be segregated as *Z. davyi*. Some post-1920 authors who have distinguished between plants respectively designated *C. floribundum* (Benth.) B. L. Rob. and *C. muhlenbergii* have based their concepts of one or the other in whole or in part on *C. tenuiflorum* (Hoffmanns. & Link) Fritsch ex Janch. *s.l.* (discussed below).

Centaurium curvistamineum (Wittr.) Druce was accepted as a species by Dunbar (1929), Abrams (1951), and Munz and Keck (1959), but was included in *C. muhlenbergii* by Piper (1906), Hitchcock (1959), Holmgren (1984), and Douglas (1999) and in *Z. muhlenbergii* by Mansion (2004). The type collection comprises small plants from Lincoln Co., Washington. Wittrock (1886) contrasted *Erythraea curvistaminea* Wittr. only with *E. douglasii* A. Gray (=*Zeltnera exaltata*; the epithet *douglasii* is illegitimate, because the species as described by Gray [1876] included the type of the older name *Cicendia exaltata* Griseb., as noted, e. g., by Broome [1973, as *Centaurium*] and Mansion [2004]), which was the only representative of the genus recorded from Washington at the time. Wittrock characterized *E. curvistaminea* by its incurved filaments that brought the anthers into contact with the stigma, which was borne on a short style that was erect from the first, thereby effecting self-pollination. He described the flowers of *E. douglasii* as differing in that the style was at first deflected in one direction and the stamens in the opposite, with both the style and the stamens later becoming erect. Broome (1973) found that floral morphology conducive to autogamy, similar to that attributed to *E. curvistaminea* by Wittrock, prevails among the smaller-flowered species now placed in *Zeltnera* and also occurs in small flowers on plants of the predominantly larger-flowered

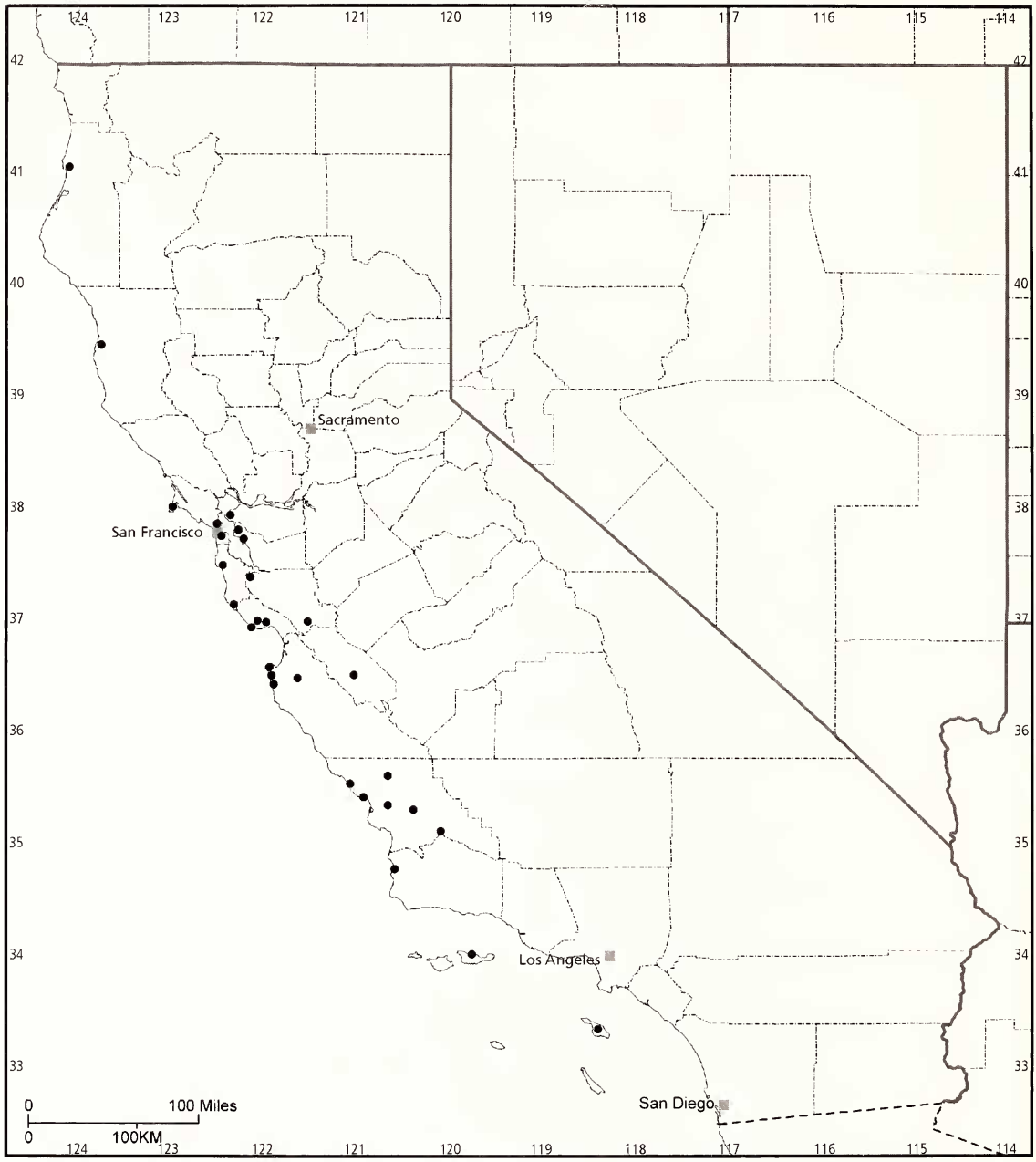

FIG. 6. Documented distribution of *Zeltnera davyi*.

species, and that the latter morphology, conducive to xenogamy, prevails among the larger-flowered species. Dunbar's (1929) and Abrams' (1951) statements that the anthers of *C. muhlenbergii*, unlike those of *C. curvistamineum*, do not spiral following anthesis may have been based on observations of newly opened flowers or on a misinterpretation of Wittrock. The anthers coil helically in all species of *Centaurium* and *Zeltnera* in North America, although not until they dehisce. From my examination of the type collection, I concur with the inclusion of *C. curvistamineum* in *Z. muhlenbergii*.

The inflorescences of *Centaurium* and *Zeltnera* species are cymes. Grisebach (1838, 1845) described *E. muhlenbergii* as having pedicellate central flowers in the dichasial divisions of the cymes. Gray (1878) and Jepson (1901, quoted

here) described *E. muhlenbergii* as having the "flowers in the forks with short pedicels or hardly any; lateral flowers with pedicels often as long as the flowers and with 2 bractlets at summit." Jepson (1925) later modified this to "flowers in the forks sessile or subsessile, the others sessile or shortly pedicelled." Gray and Jepson (in 1901) interpreted the ultimate branches of the monochasially dividing portions of the cymes, terminating in sessile flowers, as pedicels. It is the central flowers at the proximal divisions of a *Zeltnera* cyme–those "in the forks"–that are most likely to be pedicellate or to have the longest true pedicels, i.e., between the most distal bractlets and the base of the calyx. Dunbar (1929) described *C. muhlenbergii* as having pedicels absent or to 0.5 mm long and *C. curvistamineum* as having pedicels to 3 mm, whereas Howell (1939), mindful of Grisebach's description, considered pedicellate central flowers to be a distinctive trait of *C. muhlenbergii*. Abrams (1951) described *C. muhlenbergii* as having sessile flowers and *C. curvistamineum* as having all flowers on pedicels (1) 3–12 mm. In this study I have found that plants of *Z. muhlenbergii* with all of the flowers sessile or nearly so are otherwise indistinguishable from plants with at least the central flowers in the proximal cyme divisions on true pedicels usually less than 10 mm, rarely to 12 mm. No discontinuity is apparent in this variation, and neither condition appears to prevail in any part of the range of the species. Plants identified as *C. muhlenbergii* or *C. floribundum* in which all or most of the true pedicels are over 10 mm, however, are actually small plants of *Z. exaltata* or other species.

Distinction of *Zeltnera muhlenbergii* from *Centaurium tenuiflorum*

Much of the confusion associated with the names *Centaurium muhlenbergii* and *C. floribundum* is due to the absence of published reports of *C. tenuiflorum* (Fig. 7) as a naturalized species in North America prior to 1990, and the subsequent limitation of such reports to county checklists until plants from California and Texas were so designated by Mansion and Zeltner (2004). It was not included in *The Jepson Manual: Higher Plants of California* (Hickman 1993), nor by Hrusa et al. (2002) or Dean et al. (2008) in their lists of species more recently reported naturalized in California. It was recently included in the revised edition of the *Marin Flora* (Howell et al. 2007). Pending the availability of a more satisfactory classification, the name *C. tenuiflorum* is used here in a broad sense. According to Mansion et al. (2005), *C. tenuiflorum s. l.* includes a diploid entity, *C. tenuiflorum* subsp. *acutiflorum* (Schott) Zeltner; a probable autotetraploid, *C. tenuiflorum* subsp. *tenuiflorum*; and an unnamed entity believed to be an allotetraploid derivative of diploid *C. tenuiflorum* × *C. erythraea* Rafn. Of these, the first two are native to Europe and are not known from North America. The allotetraploid is a colonizing taxon, native to Europe, western Asia, and northern Africa and naturalized in Australia (Adams 1996), New Zealand (Sykes 1981), and North America.

The earliest North American specimen of *C. tenuiflorum* that I have seen is *Davy & Blasdell 5696* (UC), collected in the North Coast Ranges of California, probably in Humboldt Co., in 1896–notably, in the context of typification, decades after the names *Erythraea muhlenbergii* and *E. floribunda* had been published. The next earliest is *Jepson 2022* (JEPS), from Humboldt Co., which dates from 1902. Pre-1935 records exist only for Humboldt, Butte, and Yuba counties, California, and Douglas Co., Oregon. The earliest records from the San Francisco Bay region are from the 1940's. Except for the one record from Douglas Co., Oregon, which dates from 1916 (*Peck 3649*, GH), all known records of *C. tenuiflorum* in the Pacific states are from California (Fig. 8), but a 2005 collection from southeastern Lassen Co., California (*Ahart & Dittes 11977*, CHSC), indicates that this species is continuing to colonize new localities distant from previously known occurrences. The ranges of *C. tenuiflorum* and *Zeltnera muhlenbergii* now overlap extensively in California (Figs. 3 and 8). These species sometimes occur at the same site, without intergrading, as was the case with the *Ahart* specimens from Sutter Co., California, cited below.

Centaurium tenuiflorum and *Z. muhlenbergii* differ in branching pattern and in details of floral morphology. In *C. tenuiflorum* (Fig. 7), branching is usually restricted to the distal one-eighth to one-third of the plant. The inflorescences are densely many-flowered. The flowers are sessile, or the central flowers at the proximal divisions may be on pedicels to 1 mm or rarely to 2 mm long. Most of the flowers in each inflorescence or major division thereof are borne at nearly the same level. The inflorescences are consequently corymboid, and the aspect of the plant is often reminiscent of *Silene armeria* L. Exceptional plants of *C. tenuiflorum* are more diffusely branched. In extreme cases the plants may be branched from near the base, and large numbers of flowers may be borne in non-corymboid inflorescences, e.g., *Jepson 16757* and *19454* (JEPS). Whether such plants represent the results of viral infections, injuries, or unusual environmental conditions is not known.

The inflorescences of *Z. muhlenbergii* are more open and fewer-flowered. The flowers are borne mostly singly or in groups of two or three at several to many levels in the inflorescences, which

FIG. 7. Representative specimens of *Centaurium tenuiflorum* (*Jepson 12361*, JEPS).

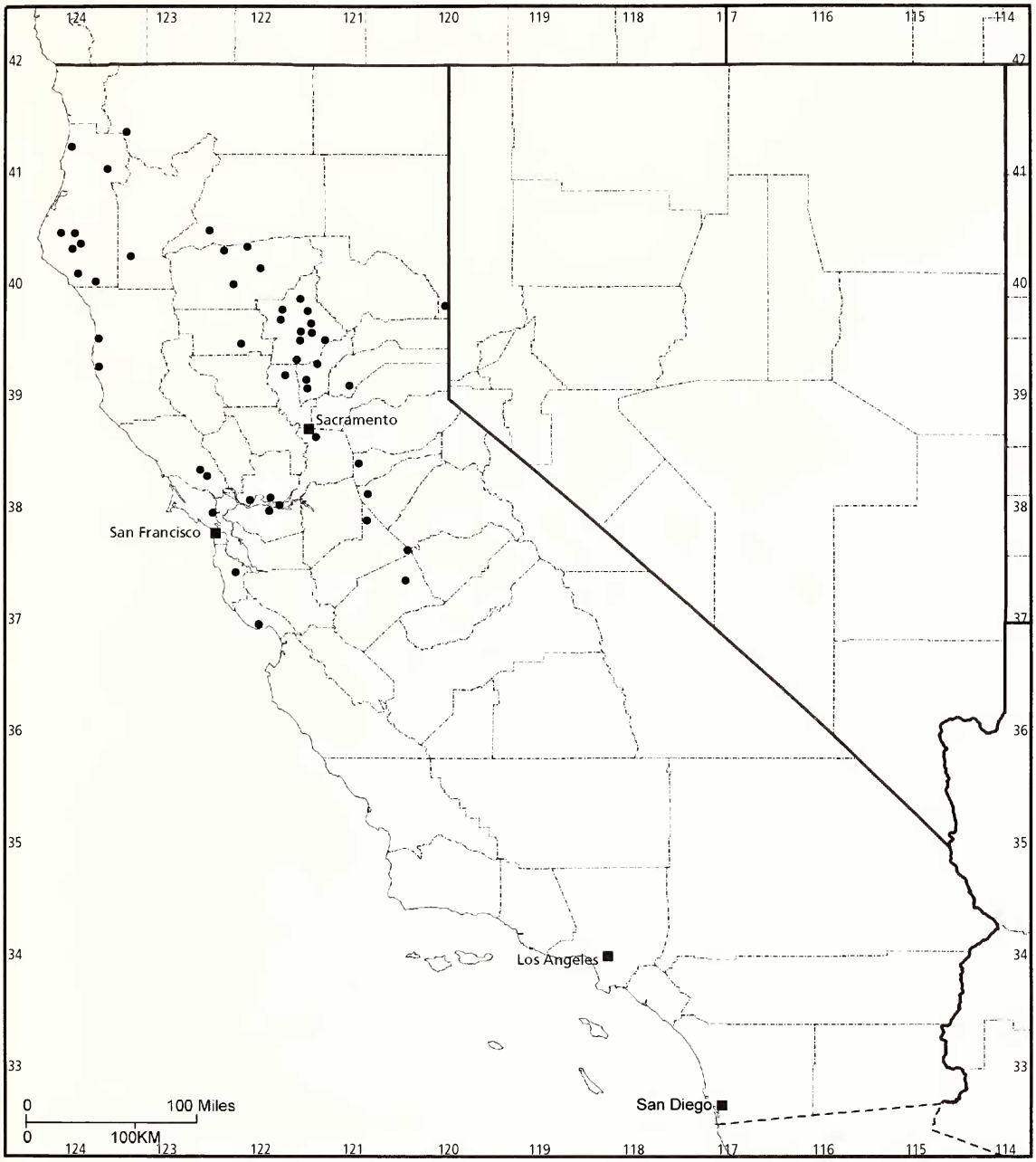

FIG. 8. Documented distribution of *Centaurium tenuiflorum* in California.

often although not invariably constitute more than half the height of the plant. The inflorescences are usually not corymboid. When they comprise only the upper quarter or less of the plant or are ± flat-topped, as occasionally occurs with relatively tall plants in densely vegetated microhabitats, even then they are more diffuse than those of *C. tenuiflorum*, and the central flowers in the proximal cyme divisions, well below the summit, are conspicuous. The difference in the branching pattern is readily observed in *Ahart 3613* (*Z. muhlenbergii*) and *3620* (*C. tenuiflorum*; both CHSC), from Sutter County, which were collected on the same date around the same vernal pool, and which comprise plants approximately the same height. The plants of *Z. muhlenbergii* are branched from near the base and the above-ground portions form, almost in their

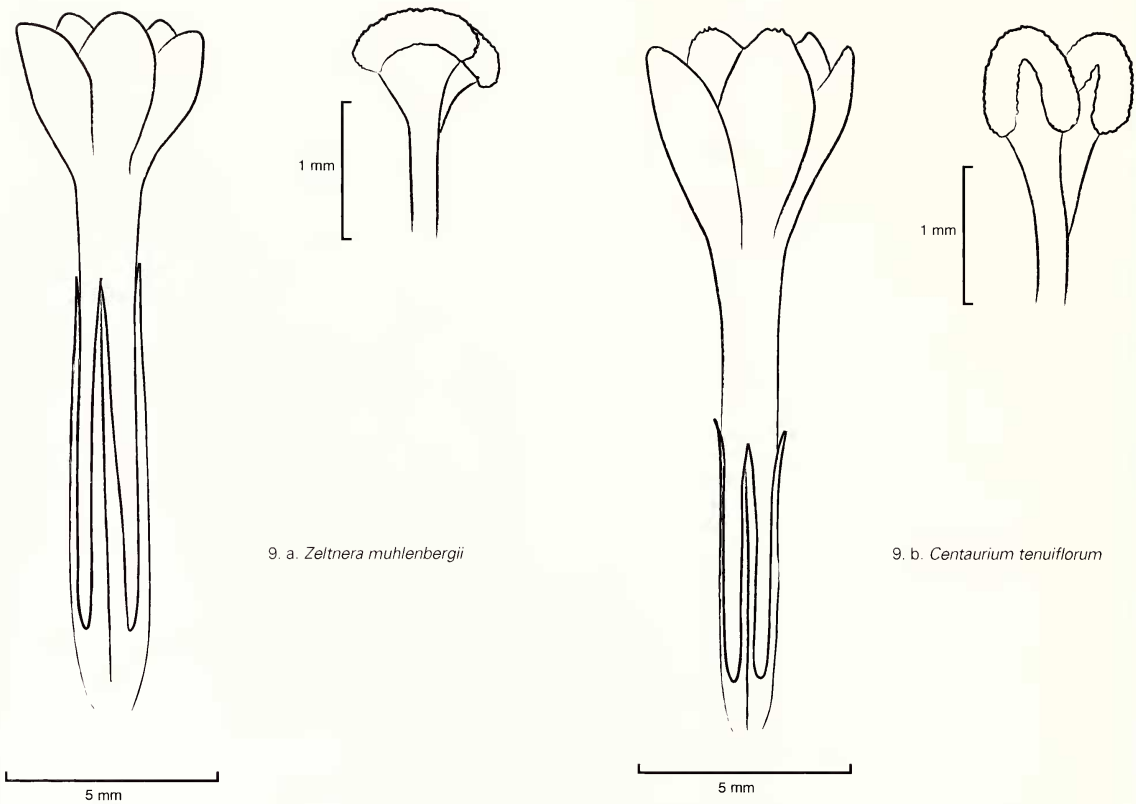

FIG. 9. Flowers (as seen in herb.) and stigmas and distal portions of styles. a. *Zeltnera muhlenbergii*; b. *Centaurium tenuiflorum*.

entirety, obconic inflorescences, whereas even these relatively small plants of *C. tenuiflorum*, the distinctness of which was recognized by the collector, Lowell Ahart, are branched only above mid-height.

The calyx lobes of *C. tenuiflorum* are acicular, tapering gradually from the base, 0.3–0.5 mm wide at mid-length and long-acuminate apically. Those of *Z. muhlenbergii* are linear-oblong, usually 0.5–0.7 mm wide at midlength and nearly parallel-sided most of their length, acute to short-acuminate at the apex (Fig. 9).

The corolla tube of a fully expanded flower of *C. tenuiflorum* is usually 1.3–2 times as long as the calyx, extending above the calyx into a slender neck from which the limb is abruptly differentiated. The corolla tube of *Z. muhlenbergii* is usually less than 1.3 times as long as the calyx, and flares less abruptly below the limb. (Flowers not fully expanded do not show these proportions, as the relative length of the corolla tube increases as the flower develops.)

Differences in the morphology of the styles and stigmas are especially useful in distinguishing *Centaurium* from *Zeltnera* species when specimens are unusually small or otherwise problematic. The styles of *Centaurium* species are shallowly bifid, the division being 0.5–0.8 mm deep in the species discussed in this paper. The stigmas are ovate, elliptic, or in Mansion's wording, "shoe-shaped," with the receptive surface forming an inverted U or V. In some *Zeltnera* species the style is undivided below the two stigmas or a single bilobed stigma, and in other species it is cleft to ca. 0.5 mm, or to 1 mm in *Z. venusta*. (A. Gray) G. Mansion, a species native to California and Baja California Norte. As noted by Mansion (2004), in accord with earlier observations by Broome (1977) and more limited observations by Grisebach (1845) and Gray (1878), the stigmas in *Zeltnera* are flabelliform, with the receptive surface reniform or lunate to nearly straight, or the stigma is single with two ± flabelliform lobes (lobing shallow or indistinct in a few species). The styles and stigmas of *C. tenuiflorum* and *Z. muhlenbergii* are contrasted in Figure 9.

Jepson, as indicated by his identifications on labels of specimens at JEPS, generally distinguished *C. tenuiflorum* from the native species treated here as *Zeltnera*, but he identified specimens of *C. tenuiflorum* as *C. umbellatum* Gilib. (a name not validly published, formerly applied to *C. erythraea* Rafn, a species native to Eurasia, naturalized in North and South Amer-

ica, Australia, and elsewhere). Joseph P. Tracy identified some his earlier specimens of *C. tenuiflorum* as *C. muhlenbergii* and some as *C. umbellatum*, but he accepted J. T. Howell's identification of some later collections of this species as *C. floribundum*. (Tracy also identified his specimens of true *Z. muhlenbergii* as *C. muhlenbergii*.) Amos A. Heller, beginning ca. 1902, may have been the first to identify specimens of *C. tenuiflorum* as *C. floribundum* (as well as being one of the first in North America to use the genus name *Centaurium*). That identification (as distinguished from the generic nomenclature) would probably have been the most likely if he had used Gray's (1886) *Synoptical Flora*. Also, the epithet *floribundum* would be more appropriate for *C. tenuiflorum* than for the species to which Bentham applied it, and early discoveries of naturalized *C. tenuiflorum* were made near Marysville, California, which, having been Hartweg's base of operations for a time, has been suggested as probably the approximate type locality of the name *C. floribundum*. (Heller's and Tracy's specimens seen in this study were those at UC plus duplicates at several other herbaria. The principal repository of Tracy's collections is UC; the principal repositories of Heller's are BKL [before 1913] and WTU [1913 and later], with duplicates widely distributed.)

The misapplication of the name *C. floribundum* to *C. tenuiflorum* prevailed from the 1920's through the 1980's. Dunbar (1929), as indicated by his citations of specimens, and subsequently Howell (1939), Abrams (1951), and Munz and Keck (1959) called this naturalized species *C. floribundum* in distinguishing it from *C. muhlenbergii*. Broome's (1973, 1978) "*C. floribundum*" from California that yielded no progeny or sterile progeny when crossed with native species, but which yielded fertile progeny when crossed with *C. tenuiflorum* from Portugal, was actually *C. tenuiflorum* (voucher specimen *Stone 3065*, DUKE). Other specimens at DUKE, JEPS, and UC further represent Broome's concept of *C. floribundum* ca. 1971–1973. Later, as discussed below, she re-identified those plants as *C. tenuiflorum*.

As early as 1948 Tracy may have suspected that plants identified by Howell as *C. floribundum* represented an introduced species, as indicated by his comment "appears as if natural" on the label of *Tracy 18109* (DAO, UC). That such plants in western North America might be naturalized *C. tenuiflorum* appears first to have been suspected by C. Rose Broome, who ca. 1978 annotated *Howell 51333* (NY) as "very likely the European species *C. tenuiflorum*...introduced & established in California [and] Oregon." Her later identifications of *C. tenuiflorum* were more definite, e.g., her annotation to *Harrison 2144* (JEPS) as "*Centaurium tenuiflorum*...a weedy European species that has become well established in California and elsewhere in the New World." Most specimens of *C. tenuiflorum* at JEPS and UC bear annotations as that species, anonymous but presumably by Broome ca. 1980, and those at MO were so annotated by her in 1992. Being limited to annotations, however, her identifications of *C. tenuiflorum* were slow to affect others' work on the genus. The first published report of *C. tenuiflorum* in North America appears to be that by Smith and Wheeler (1990), who listed *C. muhlenbergii* (rare), *C. floribundum* (infrequent), and *C. tenuiflorum* (abundant) in the flora of Mendocino Co., California. They provided no descriptions or keys, but their nomenclature and identifications probably followed Broome's and Reveal's annotations. They reported that *C. tenuiflorum* grew "in great abundance and made an impressive show" at several localities. Best et al. (1996) listed both *C. muhlenbergii* and *C. tenuiflorum* in the flora of Sonoma Co., California. In 2001 Mansion unambiguously recognized the naturalized status of *C. tenuiflorum* in North America and its affinities with Eurasian *C. tenuiflorum* and *C. erythraea*, as indicated by molecular data, although at that time he called the North American plants *C. muhlenbergii*. He later (Mansion and Zeltner 2004) identified these plants as *C. tenuiflorum*.

Although from the 1920's through the 1980's the introduced species *C. tenuiflorum* was usually called *C. floribundum* and the native *Z. muhlenbergii* was called *C. muhlenbergii*, in more recent years this usage has been reversed. Since ca. 1990, North American plants of *C. tenuiflorum* have usually been identified as *C. muhlenbergii*, and the native species has either been included with the introduced species in *C. muhlenbergii* or, when distinguished from it, called *C. floribundum*. From Holmgren's (1984) listing of the name *C. floribundum* as a heterotypic synonym of *C. muhlenbergii*, which was correct as to typification, some may have inferred that whatever had been called *C. floribundum* should henceforth be called *C. muhlenbergii*. A feedback situation probably ensued, as exemplars of "*C. muhlenbergii*" were increasingly likely to be *C. tenuiflorum* as that species became more common. Hickman's (1993) description of *C. muhlenbergii* and his reference to Humboldt Co. were based largely on *C. tenuiflorum*. He annotated both *C. tenuiflorum* and *Z. muhlenbergii* in JEPS and UC as *C. muhlenbergii*.

Because of the discrepant applications of names, descriptions of "*Centaurium muhlenbergii*" have often been based directly and/or indirectly on mixed material. Some descriptions combine wording derived from earlier works, based on true *Z. muhlenbergii*, with the later authors' own observations of *C. tenuiflorum*. Consequently, a tabular correlation of the names

used in other publications with the taxonomic equivalents accepted here has proved unfeasible. For example, the specimens cited as *C. muhlenbergii* by Jepson in 1939 represent *Z. muhlenbergii*, *Z. davyi*, and *C. tenuiflorum*.

Distinction of *Zeltnera muhlenbergii* and *Centaruium tenuiflorum* from *C. erythraea* and *C. pulchellum*

As noted above, North American specimens of *Centaurium tenuiflorum* have also been misidentified as *C. erythraea*, usually under the name *C. umbellatum*. Both *C. tenuiflorum* and *C. erythraea* have the style and stigma morphology of *Centaurium s. str.*, and both have dense, corymboid inflorescences with the flowers sessile or nearly so. The flowers of *C. tenuiflorum* are smaller than those of *C. erythraea*, with the corolla lobes 2–4.5 mm long, whereas the corolla lobes of *C. erythraea* are 4.5–8 mm. The anthers of *C. tenuiflorum* are 0.7–1.7 mm long after dehiscence; those of *C. erythraea* are 2–2.5 mm. (Exceptions to these size ranges occur in unusually small plants). Also, in *C. tenuiflorum* the basal rosette is poorly developed, usually comprising inconspicuously veined leaves smaller than the proximal cauline leaves, and is often ± withered by flowering time. In *C. erythraea* the rosette is generally well developed, comprising prominently veined leaves larger than the cauline, and is usually persistent at flowering time.

Centaurium tenuiflorum is also naturalized in the Gulf Coastal United States, from eastern Texas to Mississippi (Fig. 10). The earliest specimens from that region date from the late 1960's. Prior to a study by Holmes and Wivagg (1996), *C. tenuiflorum* in the Gulf region had been misidentified as *C. calycosum* (Buckl.) Fernald, *C. texense* (Griseb.) Fernald (these species placed in *Zeltnera* by Mansion), *C. erythraea*, and *C. pulchellum*. As Holmes and Wivagg recognized, *C. tenuiflorum* and *C. pulchellum*, which is also naturalized in that region, are sometimes similar in aspect, especially when represented by small plants. They accurately contrasted these two species, but they identified *C. tenuiflorum* as *C. muhlenbergii*. Subsequent reports of *C. muhlenbergii* in Louisiana have been based on Holmes and Wivagg's application of that name. True *Z. muhlenbergii* does not occur in the Gulf Coastal region.

As Holmes and Wivagg noted, the flowers of *C. pulchellum* are consistently pedicellate, in contrast to the sessile or subsessile flowers of *C. tenuiflorum*, although the pedicels seldom exceed 8 mm. Those of all flowers of the smallest plants of *C. pulchellum*, and sometimes all but the proximal central flowers of larger plants, may be no more than 3 mm.

European and Australian authors have generally cited plant size and branching pattern in contrasting *C. pulchellum* with *C. tenuiflorum*. Plants of *C. tenuiflorum* are usually 10–75 (90) cm tall and, as noted above, usually branch only above mid-height, from (four or) five or more nodes above the base. The branches usually diverge at less than 25°, forming a compact inflorescence. Plants of *C. pulchellum* are (2) 5–30 cm tall. At least in the larger, well-developed plants from open habitats, the lowest branches usually arise no more than three or four nodes above the base, and the branching is divaricate, to 45° or more. Each branch usually comprises a single internode, terminating in a central flower and one or two lateral branches, so that most of the plant above ground forms a largely dichasial, distally monochasial cyme. These characters, however, are variable in *Centaurium* species, being much affected by conditions of the microhabitat. Van der Sluis (1985) observed that "populations of *C. pulchellum* that grow in meadows resemble *C. tenuiflorum* in their morphological characters." In North America, plants of *C. pulchellum* seldom exceed 18 cm and are often less than 12 cm, and may not exhibit the characteristic branching pattern of the species. Such plants often have four to nine pairs of small leaves below the lowest branching. The height of the first branching above the base and the amount of branching may vary conspicuously within a single population. These species are, nevertheless, consistently different in aspect. Because of the consistently present pedicels often exceeding 1 mm and the fewer but longer inflorescence branches, the inflorescences of *C. pulchellum* appear less dense than those of *C. tenuiflorum* and not or less strongly corymboid.

As noted by Adams (1996), seed length is 0.25–0.35 mm in *C. tenuiflorum* (i.e., the allopolyploids) and 0.15–0.25 mm in *C. pulchellum*. Additional differences, supporting the acceptance of *C. tenuiflorum* as a species distinct from *C. pulchellum* although not practical for routine identification, were reported by van der Sluis (1985). He found sweroside to be the principal secoiridoid glucoside in *C. pulchellum* but only a minor component in *C. tenuiflorum*, and also reported differences in the xanthone-ß-monoglucosides.

Specimens from the Great Lakes region (GH, OSH, TRT) that had in recent years been identified as *C. tenuiflorum* were identified as *C. pulchellum* in this study.

Zeltnera muhlenbergii and *Centaurium pulchellum* can also be similar in aspect. Most reports of *C. pulchellum* in North America are from the East and the Great Lakes region. It was found in Stanislaus Co., California, in 1926 (*Howell 2021*, JEPS) and the specimen was so identified by Broome ca. 1980, but it was later annotated as *C.*

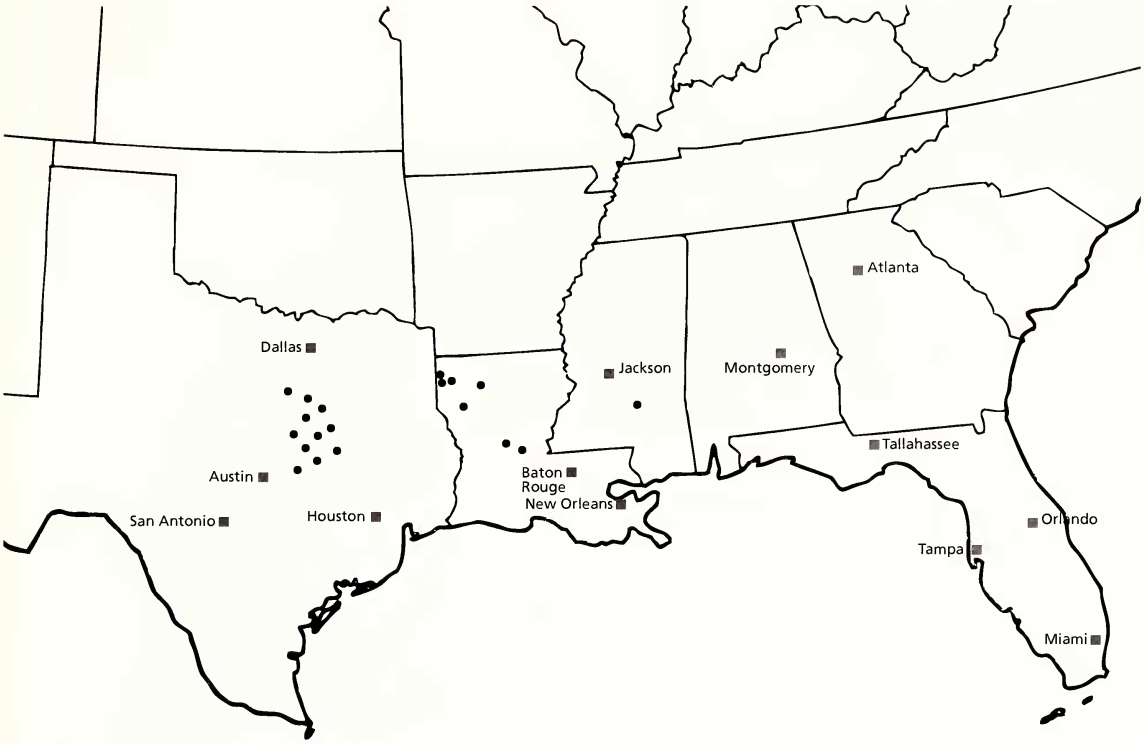

FIG. 10. Documented distribution of *Centaurium tenuiflorum* in the Gulf Coastal United States (based on Holmes and Wivagg 1996).

muhlenbergii by Hickman and the record was not reported. Its occurrence near Spokane, Washington, was detected in the present study with the identification of *Caplow 200305* (HAM). Tiny plants similar in appearance but representing two species are thus known from Spokane and Lincoln counties: *C. pulchellum* and *Z. muhlenbergii*, the latter represented by the types of the names *E. curvistaminea* and *C. muhlenbergii* var. *albiflorum* Suksd., cited below. As noted by Gray (1878), the styles and stigma lobes of *Z. muhlenbergii* and *C. pulchellum* differ as described above for the genera, those of *C. pulchellum* being similar to those of *C. tenuiflorum*.

KEY FOR DISTINGUISHING THE SPECIES DISCUSSED HERE

1 Style entire or cleft less than 0.5 mm below flabelliform stigmas with the receptive surface lunate to reniform.
  2 Mid-cauline leaves linear to narrowly elliptic or narrowly lanceolate; flowers sessile or on pedicels mostly less than 5 mm, occasionally to 12 mm; calyx lobes not keeled or with keels proximal only, less than 0.25 mm wide; corolla lobes less than 2 mm wide. . . . . *Zeltnera muhlenbergii*
  2′ Mid-cauline leaves lanceolate to elliptic or ovate; pedicels generally present, 1.5–10 (20) mm; calyx lobes keeled most of their length, keels proximally 0.3–0.6 mm wide; corolla lobes 2–3 mm wide . . . *Zeltnera davyi*

1′ Style cleft 0.5–1 mm below elliptic to ovate stigmas with the receptive surface inverted U- to V-shaped.
  3 Flowers on short but distinct pedicels 1–5 (11) mm; inflorescences diffuse, not corymboid (except sometimes on very small plants). . . . . *Centaurium pulchellum*
  3′ Flowers sessile or subsessile, no pedicels over 2 mm; inflorescences dense, corymboid.
    4 Basal rosette of leaves generally well developed and persistent at flowering time; corolla lobes (3) 3.7–8 mm. . . . . *Centaurium erythraea*
    4′ Basal rosette poorly developed and/or withered at flowering time; corolla lobes 2–3.5 (4.5) mm . . . . *Centaurium tenuiflorum*

For a key to all *Zeltnera* species see Mansion (2004).

SYNONYMY AND TYPIFICATION OF THE NAMES OF *ZELTNERA MUHLENBERGII* AND SPECIES WITH WHICH IT HAS BEEN CONFUSED

Zeltnera muhlenbergii (Griseb.) G. Mansion, Taxon 53:731. 2004. *Erythraea muhlenbergii* Griseb., gen. sp. Gent. 146. "1839" [1838], "*Muehlenbergii*"; *Erythraea ramosissima* [var.] ß *muhlenbergii* (Griseb.) O.R. Willis in Alph. Wood & O. R. Willis, New American Botanist and Florist 267. 1889, as to type only, not *sensu* Willis; *Centaurodes muhlenbergii* (Griseb.) Kuntze, Revisio Generum Plantarum 2:426.

1891. *Centaurium muhlenbergii* (Griseb.) W. F. Wight ex Piper, Contributions from the United States National Herbarium 11:449. 1906, "*Centaurion*." —Lectotype (Gillett 1963): USA, California, without locality, probably in 1831, *Douglas s.n.* (holotype K!; isotypes BM!, E, G-DC, K!, LE; photo of LE specimen JEPS!).

Erythraea floribunda Benth., Pl. Hartweg. 322. 1849; *Centaurodes floribundum* (Benth.) Kuntze, Rev. Gen. Pl. 2:426. 1891; *Centaurium floribundum* (Benth.) B. L. Rob., Proceedings of the American Academy of Arts and Sciences 45:396. 1910. —Lectotype (Jepson 1939): USA, California, E side of the Sacramento Valley, 1847, *Hartweg 405* (also numbered *1832* by Bentham; holotype K!; isotypes GH!, LD, NY!; images of LD and NY specimens on Internet!).

Erythraea tenella Nutt. ex S. Wats., United States Geological Exploration of the Fortieth Parallel, vol. 5, Botany p. 277. 1871, pro syn.; *Erythraea nuttallii* var. *tenella* A. Gray, Proceedings of the American Academy of Arts and Sciences 8:398. 1872, valid publication. —Lectotype (herein designated, following informal designation by Mansion [2004]): USA, Oregon, without locality, 1871, *Hall 425* (holotype GH!; isotypes ILL!, K!, MO!, NY!; image of NY specimen on Internet!).

Erythraea curvistaminea Wittr., Erythraea Exsiccatae, fasc. 2, no. 21. 1885 [1886?]; possibly earlier publication by same author, Botanisches Centralblatt 26: 317. 1886; *Centaurium curvistamineum* (Wittr.) Druce, Botanical Society and Exchange Club of the British Isles 1916:613. 1917; Abrams, An Illustrated Flora of the Pacific States 3:352. 1951, superfluous combination. —Lectotype (herein designated, following informal designation by Mansion [2004]): USA: Washington, Lincoln Co., Falcon Valley, 30 July 1885, *Suksdorf s.n.* (holotype S; isotypes BM!, GB, GH!, H, K, LD, MANCH, MPU, WRSL; image of LD specimen on Internet!)

Erythraea minima J. T. Howell, A Flora of Northwest America 443. 1901; *Centaurium minimum* (J. T. Howell) Piper in Piper & Beattie, Flora of the Northwest Coast 288. 1915. Specimens not cited by Howell. —Lectotype (herein designated): USA, Oregon, Washington Co., Near Hillsboro, June 1883, *Howell s.n.* (ORE, where annotated as probable holotype; image on Internet!).

Centaurium muhlenbergii var. *albiflorum* Suksd., Werdenda 1:30. 1927; *Centaurium muhlenbergii* forma *albiflorum* (Suksd.) H. St. John, Flora of Southeastern Washington and of Adjacent Idaho, ed. 1. 314. 1937. —Lectotype (herein designated, following informal designation by Mansion [2004] and customary acceptance of replicates at WS as holotypes of names first published by Suksdorf in Werdenda): USA, Washington, Spokane Co., Latah Creek SE of Spangle, 20 July 1916, *Suksdorf 8903* (holotype WS; isotypes BM!, CAS, GH!, ILL!, K!, MO!, NY!, PH, US, WS; microfiches of CAS and PH specimens MO!; images of NY and US specimens on Internet!).

Zeltnera davyi (Jeps.) G. Mansion, Taxon 53:731. 2004. *Centaurium exaltatum* var. *davyi* Jeps., A Manual of the Flowering Plants of California 762. 1925; *Centaurium davyi* (Jeps.) Abrams, An Illustrated Flora of the Pacific States 3:352. 1951. —Type (Mansion 2004): USA, California, Alameda Co., West Berkeley, 27 May 1983, *Davy 396* (incorrectly cited as *596* by Jepson), (holotype JEPS!; photo DUKE!).

Centaurium tenuiflorum (Hoffmanns. & Link) Fritsch ex Janch., Mitteilungen des Naturwissenschaftlichen Vereins der Universität Wien, ser. 2, 5:97. 1907. *Erythraea tenuiflora* Hoffmanns. & Link, Flore Portugaise 1:354. "1809" [1820]. Type not specified. The name was based on plants from Portugal; no other data were cited. The type may have been at B, subsequently destroyed (Adams 1996); not at B-Willd. Duplicates should be sought at other herbaria known to hold Hoffmannsegg's specimens. Otherwise, plate 67 in Hoffmannsegg and Link's *Flore Portugaise* (in library, MO!) can be regarded as illustrating Hoffmannsegg and Link's concept of the species.

For additional synonymy of *C. tenuiflorum* see Adams (1996).

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